

Changes in Species, Areal Cover, and Production of Moss across a Fire Chronosequence in Interior Alaska



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Contents

Abstract	1
Introduction	2
Methods	2
Site Selection	2
Net Primary Production	4
Results	7
Seasonal and Interannual Variations	7
Moss Net Primary Production in 2001	10
Summary of Findings	13
Acknowledgments	16
References Cited	16
Appendix A. Description of Data Files	20
Delta_Moss_Percent_Cover_OFR.xls	20
Delta_Moss_Growth_OFR.xls	21
Delta_Moss_Production_OFR.xls	22

Figures

Figure 1.	Map showing location of study sites, Alaska
Figure 2.	Histogram and probability curves of fractional moss cover. Data are from the Wet-1999, Wet-1885, and
Dry-1999 site	es, collected in Aug 2001, May 2003, and Aug 2003. For clarity, curves for a normal distribution are
shown for ea	ch collection time, although based on Shapiro-Wilks W Test for normality, only percent cover for May
2003 is norm	ally distributed (p>0.05)7
Figure 3.	Histogram of growth length for Hylocomium spp. based on a natural growth marker for the entire
growing seas	son 2001 and on moss stained in June 2001. Based on Shipiro-Wilk W Test for normality, all growth
increment da	ta are normally distributed (p < 0.05)
Figure 4.	Percent cover of each site in 2001. Replicate moss plots were averaged for each species within a site.
Bars are site	level standard deviations. Different letters indicate significant differences using the Tukey post-hoc test
from an analy	ysis of variance (Statistica v.6.0)11
Figure 5.	Patch NPP (pNPP) of each site in 2001. pNPP was measured by sampling growth increment and stem
density withir	n several patches at a site. Wet refers to moderately to somewhat poorly drained sites with shallow
permafrost. [Ory refers to well drained sites with no permafrost. Number shows the year that the stand most recently
burned.	12
Figure 6.	Mean area-weighted moss NPP by species across sites as summarized in table 1. Bars are standard
deviations pr	opagated from the percent cover and pNPP standard deviations (as described in the text)14
Figure 7.	The relationships of percent cover (A) and NPP (B) over log(time). While data for the wet and dry sites
are shown se	eparately, there was no significant difference between the two drainage types. Therefore, equations
shown in the	figures are for all sites combined. Error bars represent standard deviations (percent cover) or
propagated e	errors (NPP). X-axes are log scale15

Tables

Table 1.	Description of sites where moss plots were established	4
Table 2.	Moss cover, patch Net Primary Production (pNPP), and area-weighted NPP for mosses in the fire	
chronoseque	nce	9
Table 3.	Moss harvest data used to estimate patch net primary production (pNPP). Weights are oven dry	
organic matte	ər	10

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By J.W. Harden, J. Munster, K.L. Manies, M.C. Mack, and J.L. Bubier

Abstract

In an effort to characterize the species and production rates of various upland mosses and their relationship to both site drainage and time since fire, annual net primary production of six common moss species was measured. Several stands located near Delta Junction, interior Alaska, were located. These stands ranged from one to 116 years since fire in well-drained (dry) and moderately to somewhat poorly drained (wet) black spruce (*Picea mariana*)-feathermoss systems. Moss species composition varied greatly during the fire cycle, with *Ceratodon purpureus* dominating the earliest years after a fire, *Aulacomnium palustre* dominating the transitional and older stages, and *Hylocomium splendens* dominating the oldest, mature sites. *Polytrichum spp.* was found at all sites. Average moss cover ranged from <10 percent in the youngest sites to almost 90 percent in the mature sites. Species from the genus *Polytrichum* were the most productive and contributed up to 30 g m² of organic matter in one growing season. Least productive was *Rhytidium rugosum*, which contributed about 1.5 g m² of organic matter in mature stands. Recovery of moss productivity after fire was not significantly different for wet and dry sites.

Introduction

Boreal forest ecosystems are inhabited by a variety of mosses whose habitat undergoes repeated disturbance by fire. Mosses can account for significant portions of net primary production (NPP) and respiration in the boreal forest, particularly in wetlands and peatlands where vascular plants are sparse (Moore and others, 2002; Turetsky, 2003; Bubier and others, 2006). Thick moss cover, typical of many boreal forest systems, also provides an insulating layer between the soil and atmosphere (Yoshikawa and others, 2003). Therefore, moss plays both a primary role in ecosystem carbon exchange through NPP and respiration, and a secondary role by influencing thermal exchange, litter chemistry, and nutrient availability for vascular plants (Oechel and K., 1986; Proctor, 1990; Tenhunen and others, 1992; Johnson and Damman, 1993; van Breemen, 1995; Hobbie, 2000; Turetsky, 2003).

Mosses in boreal forests are particularly vulnerable to fire disturbance because most boreal fires are stand-killing fires with significant ground-fuel consumption that devastates the moss cover (Stocks and Kauffman, 1997). Although plant succession during the fire cycle has been studied and modeled for these fire-dominated systems (McGuire, 2004; Soja and others, 2004; Kasischke and others, 2006), changes in moss species have not been explicitly identified. The main goals of this study were to 1) identify dominant moss species on a variety of stand ages and soil-drainage classes within interior Alaska using measures of areal cover, and 2) quantify component net primary production of each moss species using measures of annual-growth increment by length and density.

Methods

Site Selection

Seven sites near Delta Junction, Alaska, were selected for study according to stand age and soil drainage/permafrost characteristics (fig. 1). Our well-drained "dry" sites had thin (<0.5 m) sandy or silty

mineral layers that covered a gravelly alluvial or glacial matrix with no evidence of permafrost or water table within the upper one meter. The three dry stands burned in 1999, 1987, and ~1940 (table 1). The four "wet" stands were moderately to poorly drained (Manies and others, 2004) owing in part to a thicker (>0.5 m) silt layer that covered a gravelly matrix and to the presence of permafrost within the upper one meter. Wet stands burned in 1999, 1994, 1956, and ~1885 (table 1). Carbon stocks, burn characteristics, organic chemical characteristics, and surface temperatures were found to vary with drainage class and stand age (Neff and others, 2005; Harden and others, 2006).

Black spruce (*Picea mariana*) is the dominant tree of mature stands for both dry and wet sites, but aspen (*Populus tremuloides*) is dominant or co-dominant in several of the intermediate stand ages (table 1). Understory species vary considerably among sites (Mack and others, 2008) but commonly

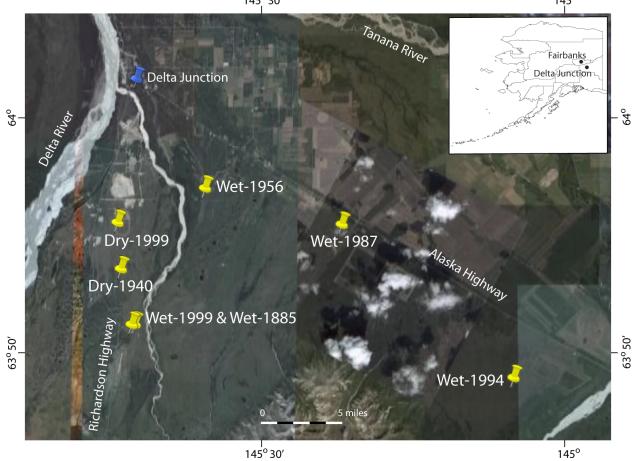


Figure 1. *Map showing location of study sites, Alaska.*

Table 1. Description of sites where moss plots were established.

See Manies and others (2004) for complete site and soil descriptions, Harden and others (2006) for soil and temperature characteristics, and Mack and others (2008) for analysis of vascular plants and plant NPP. Moss NPP values presented in Mack and others (2008) are sometimes different than the values presented here. This difference is due to changes in some values that occurred during the QA/QC process.

Last burn	Stand age in 2001 (yr)	Depth to permafrost in 2001	Organic layers	Silt layers	Dominant vascular plant in 2001			
Moderately to	o Somewhat Poor	ly Drained (Wet)						
Wet-1999	1	$70-100^{1}$	5-20	13-92	Grass			
Wet-1994	7	>25	2-10	18-29	Fireweed			
Wet-1956	44	50-140	5-7	>60	Aspen, Black Spruce			
Wet-1885	~116	40-50	13-40	70-100	Black Spruce			
Well Drained	l (Dry)							
Dry-1999	1	no permafrost	1-11	0-24	Grass			
Dry-1987	14	no permafrost	3-13	7-17	Aspen			
Dry-1940	~61	no permafrost	2-23	0-30	Black Spruce			

Active layer depth for this site was measured in 2000.

include Labrador tea (*Ledum palustre*), cranberry (*Vaccinium vitis- idaea*), blueberry (V. *uliginosum*), the grass *Festuca altaica*, and fireweed (*Epilobium angustifolium*).

Net Primary Production

At each site replicate moss plots were arranged along linear transects with plots spaced every 20 to 40 m. In some cases, plots were damaged by wildlife trampling or were added for other research efforts; therefore, replicate plots vary from nine to 15. A PVC square was used to construct 60 cm² moss plots using string anchored by large nails into the soil. At two sites, Dry-1999 and Dry-1940, 100 cm² plots from another study (Liu and others, 2005) were used instead. These moss plots were used to measure the percentage of moss cover.

The percentage of moss cover was recorded in August 2001, May 2003, and August 2003. Moss parcels (polygons) within each moss plot, in which one or two mosses were dominant, were delineated

on the ground with cotton swabs or flagging, to help demarcate boundaries between polygons, and then sketched in a field notebook (appendix A). Digital photographs were taken from above and mostly parallel to the moss surface. ArcMap software (ArcGIS v. 8, ESRI, Inc.) was used to differentiate polygons within each photo and to quantify the percentage of areal cover for each moss species at each moss plot. The moss species present were *Aulacomnium palustre*, *Ceratodon purpureus*, *Dicranum* spp., *Hylocomium splendens*, *Pleurozium schreberi*, *Polytrichum* spp., and *Rhytidium rugosum*.

Growth dimensions for each moss were based on growth between June and September of 2001. Moss was dyed with a fluorescent brightener (Dye no. 28 from Sigma Company; catalog item F 3543) in locations with dense, generally unmixed mosses (appendix A). Application of the dye to the moss required a very dry substrate (no rain for about two to three weeks) which occurred in early June. We applied the dye in a thin, even layer on a 10 cm² square using a spray bottle. *Ceratodon purpureus* was not dyed because of its extremely thin growth structure. *Dicranum* spp. did not retain the dye. Sprayed moss samples were harvested in late September using an ~5-cm diameter core and stored in a tin or hard plastic container so that they retained their original height. Samples were kept refrigerated until measured.

In the lab, we measured the length of new growth of each stem individually (referred to as growth increment) under a black light using a caliper. After recording the growth increment, this new growth was harvested and placed into a labeled container. Growth increment for *Hylocomium splendens* was also measured using its natural growth marker (Callaghan and others, 1978; Okland, 1995), which is identified by a growth direction lateral to the main axis of previous growth. In this way we were able to test the natural marker against our measurements (see Results). Harvested materials were air dried; weights were converted to an oven dry basis by using a representative moisture sample. Production

Increment (P, g stem⁻¹), which includes growth of both the stem and leaves, was calculated from the moss-dye harvests as the total mass of new growth (g) divided by number of stems.

Stem density (D; stems m⁻²) was determined from the above samples, as well as an additional three samples. These three samples were cored outside the moss-dye plots in September 2001 in a variety of shading environments in order to robustly characterize stem density of the dominant species at each study site (appendix A). Patch net primary production (pNPP, in g m⁻², see eq. 1) is defined as the growth within a homogenous patch of moss and is based on both the dyed production increment (P) and stem density harvests (D). Net primary production (NPP_a , eq. 2) of moss species a is the product of patch NPP and percent areal cover.

$$pNPP_a (g m^{-2}) = P_a (g stem^{-1}) * D_a (stem m^{-2})$$
 (Eq. 1)

$$NPP_a (g m^{-2}) = pNPP_a (g m^{-2}) * A_a (percent)$$
 (Eq. 2)

where $pNPP_a$ is the net primary production of moss species a in a homogenous patch; P_a is the production increment for moss a as determined by the oven-dried weight (g) of new growth divided by number of stems; D_a is the number of stems (m⁻²) for moss a or stem density; A_a (percent) is the areal coverage of moss a; and NPP_a (g m⁻²) is the area-weighted Net Primary Production of moss a.

Standard deviations of stem density (D_a) and growth increment (P_a) were calculated from replicate core samples from each site. In cases where a moss species was present at a study site but did not have a pNPP value, the average pNPP of other sites was used. Standard deviations for site level pNPP values and NPP_a were calculated using propagation of errors. This formula calculates the error of NPP_a as a function of the relative standard deviation of pNPP and areal coverage for species a.

There were two species for which no field-growth data were available, *Ceratodon purpureus* and *Dicranum* spp. For *Ceratodon purpureus*, we calculated *pNPP* from biomass harvests at Dry-1999 done as a part of another study (Mack and others, 2008). Based on changes in moss biomass from 2001 to

2002, pNPP was 20 ± 45 g m⁻² yr⁻¹. We did not estimate pNPP for *Dicranum* spp. because the coverage was usually less than three percent.

Statistical analyses, including Analysis of Variance (ANOVA), regression, and Wilks lambda testing of means, were performed using Statistica (v. 6.0, Statsoft Inc.).

Results

Seasonal and Interannual Variations

Moss cover did not differ between May 2003 (mean of 26 ± 14 percent (1 σ)) and August 2003 (mean of 42 ± 38 percent) at the Dry- and Wet-1999 burn sites (fig. 2). Total moss cover in August 2001 (mean of 45 ± 43 percent) was not significantly different from that of August 2003 (42 ± 38 percent),

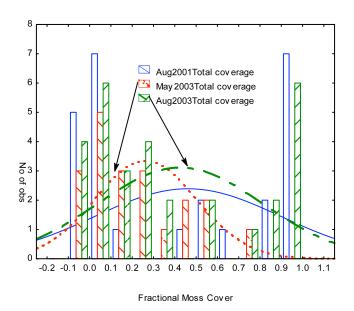


Figure 2. Histogram and probability curves of fractional moss cover. Data are from the Wet-1999, Wet-1885, and Dry-1999 sites, collected in Aug 2001, May 2003, and Aug 2003. For clarity, curves for a normal distribution are shown for each collection time, although based on Shapiro-Wilks W Test for normality, only percent cover for May 2003 is normally distributed (p>0.05).

based on the nonparametric Wilcox test for matched pairs ($T_n=50=32$, Z=2.1, p=0.035). Standard deviations for percent cover typically exceeded the average value for any given moss species (table 2).

Growth increment determined by the natural marker method for *Hylocomium* splendens resulted in significantly longer stems $(15.7 \pm 5.6 \text{ cm})$ than by the stained method $(7.6 \pm 3.8 \text{ cm})$ (fig. 3; Wilks lambda test for site means 0.9248, F (4, 862) = 8.58, where p=<0.0001). This difference likely represents the late (June) application of the dye, suggesting that significant growth length occurred before June. Nevertheless, the stained method was used for growth increment (G, cm) and production increments $(P, \text{g m}^{-2})$ for not only *Hylocomium splendens* but for the other mosses as well. Therefore, our results represent minimum estimates of growth.

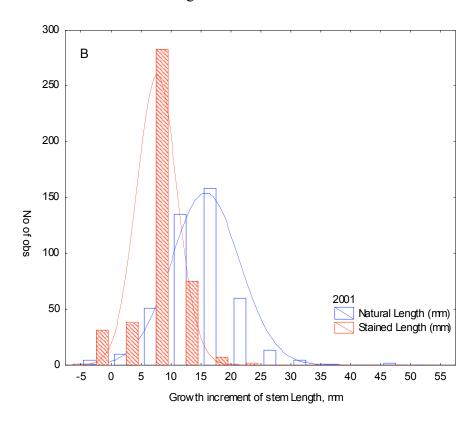


Figure 3. Histogram of growth length for Hylocomium spp. based on a natural growth marker for the entire growing season 2001 and on moss stained in June 2001. Based on Shipiro-Wilk W Test for normality, all growth increment data are normally distributed (p < 0.05).

Moss cover, patch Net Primary Production (pNPP), and area-weighted NPP for mosses in the fire chronosequence.

[MD, missing data]

Site	Moss species	cies Percent Cover		Patch NPP (pNPP)			NPP			
		%	(SD)	n	$g m^{-2}$	(SD)	n	g m ⁻²	(SD)	n
Wet-1999	Ceratodon	0.5	(0.8)	13	20.0**	(45.0)	4	0.1	(2.8)	4
Wet-1999	Dicranum	0.6	(0.8)	13	MD			MD		
Wet-1999	Polytrichum	4.2	(7.9)	13	142.2	(30.5)	5	6.0	(1.9)	5
Wet-1994	Ceratodon	58.2	(26.2)	10	20.0**	(45.0)	4	11.6	(2.3)	4
Wet-1994	Dicranum	8.9	(14.7)	10	MD			MD		
Wet-1994	Polytrichum	9.5	(14.4)	10	122.4*	(56.0)	14	11.6	(1.6)	10
Wet-1956	Aulacomnium	43.9	(43.0)	9	48.8	(22.9)	5	21.4	(1.1)	5
Wet-1956	Dicranum	0.9	(2.7)	9	MD			MD		
Wet-1956	Hylocomium	8.9	(13.7)	9	33.6	(17.6)	5	3.0	(1.6)	5
Wet-1956	Polytrichum	1.4	(2.5)	9	122.4*	(56.0)	14	1.8	(1.8)	9
Wet-1956	Rhytidium	1.1	(3.3)	9	36.6*	(14.3)	9	0.4	(3.0)	9
Wet-1885	Aulacomnium	22.8	(27.7)	9	52.7	(9.7)	4	12.0	(1.2)	4
Wet-1885	Dicranum	0.9	(1.4)	9	MD			MD		
Wet-1885	Hylocomium	45.1	(32.5)	9	34.1	(7.0)	3	15.4	(0.7)	3
Wet-1885	Pleurozium	7.8	(23.3)	9	30.1	(19.3)	2	2.3	(3.1)	2
Wet-1885	Polytrichum	7.0	(9.9)	9	132.7	(78.5)	4	9.3	(1.5)	4
Wet-1885	Rhytidium	3.9	(6.5)	9	40.0	(18.0)	5	1.6	(1.7)	5
Dry-1999	Ceratodon	2.8	(3.9)	15	20.0**	(45.0)	4	0.6	(2.6)	4
Dry-1999	Dicranum	2.8	(3.9)	15	MD			MD		
Dry-1999	Polytrichum	0.1	(0.3)	15	122.4*	(56.0)	14	0.1	(3.0)	14
Dry-1987	Ceratodon	25.4	(16.7)	9	20.0**	(45.0)	4	5.2	(2.3)	4
Dry-1987	Polytrichum	31.8	(22.0)	9	94.4	(55.5)	5	30.0	(0.9)	5
Dry-1940	Dicranum	3.1	(6.4)	10	MD			MD		
Dry-1940	Hylocomium	51.0	(28.7)	10	37.2	(12.3)	5	19.0	(0.7)	5
Dry-1940	Pleurozium	2.0	(6.3)	10	25.2*	(16.0)	3	0.5	(3.2)	3
Dry-1940	Polytrichum	7.1	(22.5)	10	122.4*	(56.0)	14	8.7	(3.2)	10
Dry-1940	Rhytidium	4.3	(9.6)	10	32.4	(8.5)	4	1.4	(2.3)	4

^{*}The average pNPP of all sites was used, as production increment (P) samples were not collected for this species at this site.

**Values based on changes in moss biomass data from 2001 to 2002 (M. Mack, personal communication).

Table 3. Moss harvest data used to estimate patch net primary production (*pNPP*). Weights are oven dry organic matter.

Site	Moss type	Stem density (<i>D</i>)			Growth increment (<i>G</i>)			Production increment (P)		
		$10^3 per$ m^2	(SD)	n	cm	(SD)	n	g per stem *10 ³	(SD)	n
Wet-1999	Polytrichum	29	(9)	8	1.05	(0.20)	5	4.47	(1.21)	5
Wet-1956	Aulacomnium	86	(35)	8	0.69	(0.12)	5	0.60	(0.11)	5
	Hylocomium	17	(9)	8	0.82	(0.24)	5	2.19	(1.40)	5
	Pleurozium	13	()	(1)	0.49	()	(1)	1.21	()	1
Wet-1885	Aulacomnium	89	(27)	7	0.66	(0.17)	4	0.50	(0.09)	4
	Hylocomium	17	(9)	6	0.80	(0.11)	3	1.49	(0.13)	3
	Pleurozium	27	(13)	5	0.59	(0.06)	2	1.05	(0.08)	2
	Polytrichum	19	(7)	7	1.30	(0.73)	4	6.31	(3.15)	4
	Rhytidium	42	(23)	8	0.52	(0.09)	5	0.79	(0.21)	5
Dry-1987	Polytrichum	24	(12)	8	0.73	(0.12)	5	4.09	(0.80)	5
Dry-1940	Hylocomium	18	(6)	8	0.69	(0.16)	5	2.30	(0.64)	5
	Rhytidium	32	(9)	7	0.58	(0.12)	4	1.06	(0.14)	4

For sites of various stand ages (fire chronosequence), measurements of total moss cover taken in 2001 ranged from <10 percent on the newest burns to as much as 90 percent on the mature control sites (table 3; fig. 4). Moss cover was best modeled by the following equation ($r^2 = 0.69$):

Moss Percent Cover =
$$16.7 * \text{Log}_{e}(\text{Years since fire}) + 6.3$$
 (Eq. 3)

Moss Net Primary Production in 2001

Average growth increment (*G*) and stem density (*D*) varied greatly among mosses. Growth increment ranged from <0.5 cm for *Pleurozium* spp. to more than 1 cm for *Polytrichum* spp. (table 3). The growth increment for *Polytrichum* spp. ranged from 0.73–1.30 cm per year (table 3), which is within the range of growth rates for *Polytrichum* spp. throughout Canada. The growth increments of *Hylocomium splendens* and *Polytrichum* spp., the only mosses that occurred in most of the sites, did vary some among different sites, but less so than the variations among moss species within a site (table

3). Stem density ranged from 13,000–89,000 stems per m⁻² and was greatest for *Aulacomnium palustre* (table 3). Production increment also ranged greatly (by 1000 fold) among moss species and was greatest for *Polytrichum* spp. (>4000 g stem⁻¹ yr⁻¹; table 3).

Patch net primary production (*pNPP*) represents site-specific growth rates of individual mosses. *Ceratodon purpureus* and *Polytrichum* spp. dominated the cover in new burns (fig. 4). *Polytrichum* spp. played an important role in the *pNPP* of all sites (fig. 5). At the Wet-1885 site, the moss with the highest

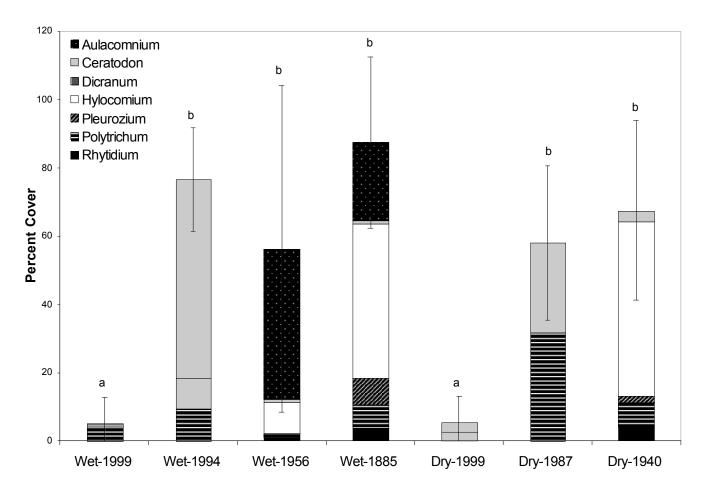


Figure 4. Percent cover of each site in 2001. Replicate moss plots were averaged for each species within a site. Bars are site level standard deviations. Different letters indicate significant differences using the Tukey post-hoc test from an analysis of variance (Statistica v.6.0).

growth rate (pNPP) was Polytrichum spp. with >130 g m-2 of growth. This rate is at least two times higher than for any other moss species (fig., table 3) in this study area. Growth rates (*pNPP*) for *Hylocomium splendens*, were 34 to 37 g m-2 (table 3), which is at the low end of growth rates found throughout Canada (Vitt, 1990; Bisbee and others, 2001; Turetsky, 2003).

Ceratodon purpureus and Polytrichum spp. dominated total moss production (NPP) in the earliest years after a fire, Aulacomnium palustre dominated the transition and older stages, and

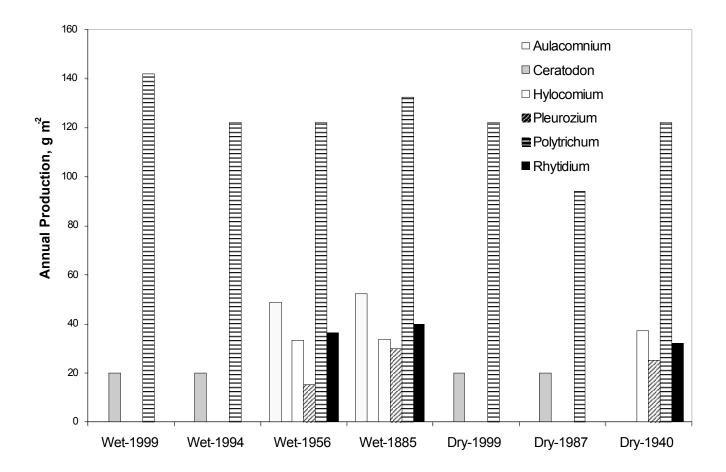


Figure 5. Patch NPP (pNPP) of each site in 2001. pNPP was measured by sampling growth increment and stem density within several patches at a site. Wet refers to moderately to somewhat poorly drained sites with shallow permafrost. Dry refers to well drained sites with no permafrost. Number shows the year that the stand most recently burned.

Hylocomium splendens dominated the oldest, mature sites (fig. 6). Polytrichum spp. was found at all sites and contributed between 7 to 99 percent of total moss production (fig. 6).

The relationships of moss cover and NPP over time were not linear. Therefore, stand age was transformed using log₁₀. For both percent cover and NPP, the semi log regression equations for the wet and dry sites were not significantly different from each other. Therefore, all sites were combined when modeling the recovery of percent cover or NPP over time (fig. 7a,b).

Summary of Findings

- Moss NPP in the Delta Junction region:
 - Total NPP, which includes changes in both upward and lateral growth, ranges from near zero to at least 41 g m⁻² y⁻¹ (figs. 6 and 7b) depending on stand age.
 - o *Polytrichum* spp. had the highest production in upward growth in all sites (table 3).
 - The comparison of dyed versus natural marker growth estimates for *Hylocomium splendens* suggests that a significant portion of moss growth occurs before June (fig. 3).
- Sensitivity of moss species and production to soil drainage/permafrost:
 - o Species composition differs between wet and dry mature stands (fig. 4).
 - There were no significant differences in moss cover or moss production between wet and dry mature stands (fig. 7).
- Sensitivity of moss species and production to stand age:
 - Polytrichum spp. and Ceratodon purpureus comprise most of the production (NPP) in recently burned sites (fig. 6).
 - Aulacomnium palustre, Hylocomium splendens, and Polytrichum spp. dominate production
 (NPP) in moderate to mature stands (fig. 6).

 \circ Moss production increased exponentially over stand age from near zero in burned stands to \sim 41 g m⁻² y⁻¹ in mature stands (fig. 7).

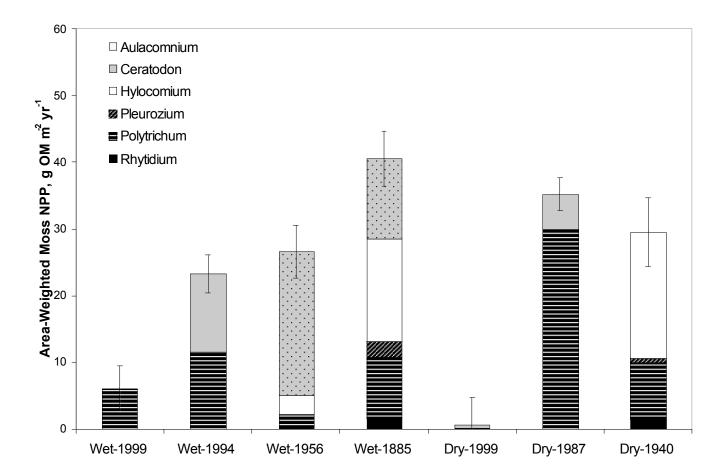


Figure 6. Mean area-weighted moss NPP by species across sites as summarized in table 1. Bars are standard deviations propagated from the percent cover and pNPP standard deviations (as described in the text).

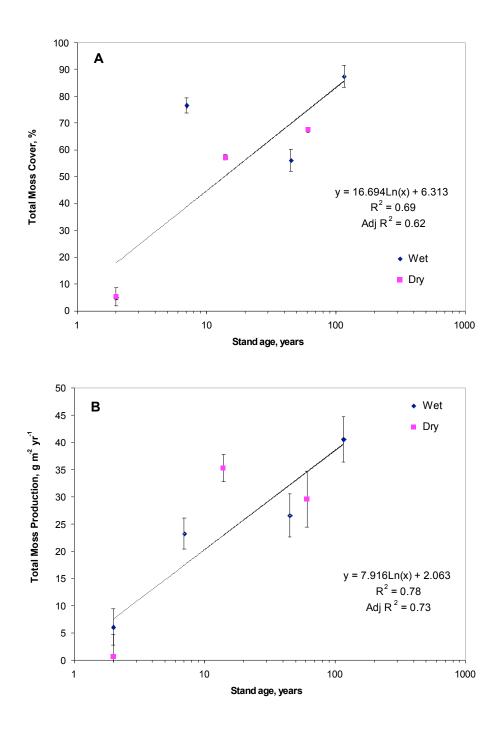


Figure 7. The relationships of percent cover (A) and NPP (B) over log(time). While data for the wet and dry sites are shown separately, there was no significant difference between the two drainage types. Therefore, equations shown in the figures are for all sites combined. Error bars represent standard deviations (percent cover) or propagated errors (NPP). X-axes are log scale.

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Appendix A. Description of Data Files

Three Excel data files accompany this report. These files contain the raw data that were used to calculate the results presented in this report. In some of the files, the data are represented with their field IDs, not the publication IDs. The corresponding values are Wet-1999 = DFCB, Wet-1956 = DF56, Wet-1885 = DFCC, Dry 1999 = DFTB, Dry-1987 = DF87, and Dry-1940 = DFTC.

Delta_Moss_Percent_Cover_OFR.xls

The data within this file represent the percentage of areal cover of the different moss species, lichen, and nonvegetative cover (bare ground, wood, and/or litter) found within each moss plot. These data were calculated from photographs for each moss plot. Moss parcels (polygons) in which only one or two mosses were dominant were delineated within each moss plot using colored Q-tips or flagging. The amount of each moss species (percent) within each moss polygon was noted on a field sheet. The different polygons within each moss plot were also sketched on the field sheet. Digital photographs were then taken from above and mostly parallel to the moss surface of the marked moss plot.

The photograph for each moss plot (column B) within each site (column A) was imported into ArcMap software (ArcGIS v. 8, ESRI, Inc.). Each moss plot was processed individually using the following procedure. First, the corners of each moss plot were assigned *x* and *y* values in proportion to the size of the moss plot (60 cm or 100 cm long sides). This procedure scaled shapes within the image appropriately. The perimeter of each marked moss polygon was then outlined using the polygon tool. The area of each polygon was automatically calculated by the ArcMap program; this area value was multiplied by the percentage of each moss species and/or lichen within the polygon. These polygon percent cover values were then summed to determine the total percent cover (percent) of each moss species and/or lichen (columns C – I, column K) found within the plot (column B). The remaining area was assumed to be bare ground, wood, and/or litter (column L). Two columns, total moss (percent,

column J) and total percent cover (percent, column M) were calculated as the sum of the moss or moss, lichen, and bare/wood/litter columns, respectively. The processing notes column (N) contains information about the confidence of the data processing steps and any assumptions made.

Delta_Moss_Growth_OFR.xls

The data within this file represent the growth increments measured for individual moss species (column C) within each site (column A). Small patches of moss close, but not adjacent to, the actual moss plots (column B) were dyed in June of 2001 with a fluorescent brightener (Dye no. 28 from Sigma Company; catalog item F 3543). These patches were generally dense patches of an individual species of moss. Application of the dye to the moss required a very dry substrate (no rain for about two to three weeks) which occurred in early June. The dye was applied in a thin, even layer on a 10 cm² square using a spray bottle.

These patches of moss were relocated in late September and harvested using an ~5-cm diameter core. The moss sample was carefully removed and placed into a plastic or aluminum container in such a way that the sample retained its original height and structure. Samples were shipped back to the lab and kept refrigerated until measured.

Samples were processed stem-by-stem under a black light. New growth was defined as the upper part of each stem without fluorescent reflectance. This new growth was measured (column D), harvested, and placed within a tin for drying. Annual growth for *Hylocomium* sp. was also measured using natural markers (column E) assuming that new growth was represented by the last 'stair-step' of each live stem (Callaghan and others, 1978). Notes regarding storage or processing are found in column F.

Delta_Moss_Production_OFR.xls

The data within this file represent the growth increments measured for individual moss species (column C) within each site (column A). Two sets of sample types are included in this file.

The first samples are from small patches of moss close, but not adjacent to, the actual moss plots (column B) that were measured for growth (column D = growth; see section above,

Delta_Moss_Growth_OFR.xls). These samples have data on number of stems per sample (column E),

average growth increment per stem (mm; column I, raw data in Delta_Moss_Growth_OFR.xls), and the

mass of this growth (g, oven dried basis; column H). The second set of samples (column D = stem

count) were taken outside the moss-dye plots in September 2001 in a variety of shading environments in

order to robustly characterize stem density of the dominant species at each study site. These samples

were obtained with the same ~5 cm corer used for the growth samples.

The remaining columns are calculated based on the data discussed above. Stem density (stems m⁻²; column F) was calculated as the number of stems per core (column E) times the area of the core ([II * (4.8 cm diameter corer/2)²] and then converted to m². This value was then converted to the same units as used in Table 3 (stems * 10³ m⁻²; column G). Similarly, growth increment (column I, mm) was converted to cm (column J). Production increment (g stem⁻¹; column K) is the growth mass (g; column H) divided by the number of stems (column E). This value was converted to the same units as used in Table 3 (g stem⁻¹ * 10⁻³) in column L. Patch NPP (g m⁻²; column M) is the product of the Production Increment (g stem⁻¹; column K) and Stem Density (stems m⁻²; column F).